HORIZONS

Linking zooplankton communities to ecosystem functioning: toward an effect-trait framework

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The renewed interest in trait-based approaches has offered a stimulating, conceptual framework for predicting species distributions, assessing community composition and determining biodiversity–ecosystem linkages. However, despite previous attempts to clarify trait terminology and its application, selecting ecologically meaningful traits that mechanistically link levels of biological organization remains a challenge in aquatic ecology. Response traits can be used to capture community assembly processes along environmental gradients, while effect traits hold the potential to predict ecosystem functions. Although effect traits related to organismal physiology and body composition best allow for extrapolation from individuals to ecosystem processes, such traits are still rarely incorporated within plankton functional approaches or classifications for numerous reasons. Synthesizing current knowledge on effect traits in zooplankton, we call for a better implementation of such metrics as descriptors of community structure. We then capitalize on concepts of bioenergetics and ecosystem ecology to propose a hierarchical framework for zooplankton trait classification, identifying key traits fulfilling organismal functions and linking these to ecosystem processes likely to be influenced. Our framework provides insight regarding trait trade-offs, with implications for feedbacks to ecosystems, aiming to bridge the gap between plankton community ecology and aquatic biogeochemistry.

KEYWORDS: body size; ecophysiology; ecosystem function; energy budget; functional traits; trade-offs

INTRODUCTION

Traits are fundamental descriptors of organismal phenotype, functionality and performance (Arnold, 1983). Their use in ecology provides a framework that enables the linking of different levels of biological organization, from individual morphology and activity to the dynamics of food webs and ecosystems (Chapin et al., 1996; Violle et al., 2007). In population and community ecology, traits have served to generalize across species to better address mechanisms of assembly, coexistence and reactivity (Sæther and Bakke, 2000; McGill et al., 2006). Compelling evidence has since accumulated for the relevance of a trait-based approach in organism–ecosystem linkages in terrestrial ecosystems (Eviner and Chapin, 2003; Hooper et al., 2005; de Bello et al., 2010), prompting analogous investigations in aquatic environments (Giller et al., 2004; Yvon-Durocher and Allen, 2012), with some studies highlighting the promising use of plankton traits (Litchman et al., 2007; Merico et al., 2009; Zwart et al. 2015). However, from an ecosystem perspective, the wide variety of plankton traits identified are not equally useful for larger-scale implications. A critical point in deriving trait-based indicators of ecosystem functioning lies in meaningfully choosing traits or trait types (Petchey and Gaston, 2006), which may sometimes be erroneously perceived as a trivial step.

Currently, trait choice remains constrained by the amount of information available and the cost of new observations (Gayraud et al., 2003), and while traits can characterize species performance, responses and interactions, fewer have been directly linked to specific ecosystem processes. It is important to recognize that traits may differentially affect multiple ecosystem functions, with some being more or less directly linked to a specific process, and others only exerting indirect effects (Lavorel and Garnier, 2002). Further, including traits that are not explicitly, nor directly related to an ecosystem function of interest may potentially introduce bias and spurious relationships in analyses, thereby hindering the detection of true ecological linkages. As a result, the traits chosen for inclusion in biodiversity studies (functional diversity; biodiversity–ecosystem function relations) or ecosystem models can affect conclusions. Therefore, it has been recommended that the nature, type and even number of traits used in such approaches be carefully selected based on the particular aims of a study (Petchey and Gaston, 2002, 2006).

Over the last decade, numerous plankton traits have been described for many taxa and their use has been increasingly encouraged to characterize the community structure of both phytoplankton (Reynolds et al., 2002; Litchman and Klausmeier, 2008; Litchman et al., 2010) and zooplankton (Barnett et al., 2007; Kiørboe, 2011; Litchman et al., 2013). Many such studies focus on categorical or qualitative traits related to individual performance and behaviour, with implications mostly at individual, population or community levels, whereas quantitative traits directly affecting ecosystem processes are either absent or poorly represented. Indeed, the link between individual traits characterizing community structure and how these contribute concretely to aggregate processes has been weakly established to date, especially for zooplankton, in part owing to the non-quantitative nature of most plankton traits that have wide species coverage (Barnett et al., 2007; Litchman et al., 2013). Quantitative traits such as zooplankton size, body composition/requirements or physiological measurements of elemental fluxes (e.g. observations related to functions of excretion, egestion, respiration, growth, etc.) are best suited for extrapolation from organisms to ecosystem stocks and fluxes of material, and should thus be the focus of studies linking plankton individuals and communities to ecosystems.

Our objective here is to bring the discussion of plankton functional traits, formal descriptors of species' ecological roles (Díaz and Cabido, 2001), back into the framework of *response* and *effect* traits (Lavorel and Garnier, 2002; Nock et al., 2016). We argue that this framework must be adopted to: (i) preserve consistency and improve dialogue with other subfields of trait-based ecology, thereby facilitating future comparison, generalization and synthesis; (ii) better clarify the rationale for trait selection with respect to a study's objectives; and (iii) derive more mechanistic relationships between plankton community structure and ecosystem functioning. While the response and effect trait framework has been implemented and applied widely in terrestrial studies, it is our contention that it is still not commonly used in aquatic ecology, especially for plankton. In particular, despite the recognized relevance of many zooplankton traits for biogeochemical processes, including a considerable amount of trait data available in the literature, most of these effect traits have yet to be incorporated within a functional trait context. By synthesizing effect traits in zooplankton, we revisit the relevance of zooplankton stoichiometry and physiology in an effect trait-based framework, and emphasize the use of body size as a proxy for traits that are more difficult to measure. Finally, we propose a functional classification scheme based on both organismal and ecosystem functions, identifying key traits for linking these two levels of organization.

FUNCTIONAL TRAITS AND THEIR RELEVANCE ACROSS LEVELS OF BIOLOGICAL ORGANIZATION

Response versus effect traits

An appreciable number of definitions for traits, functional traits and trait types exist in the current ecological literature (for plankton examples, see: Le Quéré *et al.*, 2005; Litchman *et al.*, 2007, 2010, 2013). Defined most simply, traits are measurements of behavioural, molecular, morphological, phenological or physiological features of organisms, all of which are, and must be, measured at the organismal level (Violle *et al.*, 2007). Traits have long been used to anatomically describe and classify species (e.g. taxonomy) and to link individual variation with fitness (e.g. in evolutionary ecology). However, it is only relatively recently that the concept of "functional traits" has emerged, which aims to describe species in terms of their ecological roles based on how they interact with each other and with their environment (Chapin *et al.*, 1996; Díaz and Cabido, 2001). Functional traits are now part of a multi-scale framework using species' responses and effects within a tropho-dynamic and evolutionary context, with respect to scenarios of climate and other anthropogenically-induced changes (Díaz *et al.*, 2007; Thomas *et al.*, 2016). While functional traits are properties of organisms, reflecting individual performance and fitness (e.g. life-history traits), they can also encapsulate information on population dynamics (i.e. demographic traits), community response mechanisms to changing conditions (through relative abundance fluctuations) and realized food web interactions (i.e. response traits), and ultimately indicate emerging properties of ecosystems (i.e. effect traits; Fig. 1; for additional examples, see Violle *et al.*, 2007). Thus, response and effect trait types can respectively be used to model species' fitness and niches as a function of biotic or abiotic conditions (Kearney and Porter, 2009), and to document organisms' contributions to ecosystem function (Lavorel and Garnier, 2002). That said, some traits are more versatile than others, affecting processes at multiple ecological scales, and thus falling into more than one category of trait type; for example, in a response and effect trait framework, traits such as size and growth rate could be considered as either a response or effect type (Fig. 1).

For plankton, ecologists have thus far focused primarily on response traits, which are useful to assess species interactions and community succession as a function of environmental conditions (Barnett and Beisner, 2007; Merico *et al.*, 2009; Beisner and Longhi, 2013). This has been especially the case for phytoplankton, for which quantitative trait measurements are becoming increasingly available (e.g. Edwards *et al.*, 2015). For example, phytoplankton response traits have been shown to predict dominance amongst species based on their resource competitive abilities (Edwards *et al.*, 2013a, 2013b). Having been the focus, this trait type now forms the core of the emergent field of functional biogeography, which aims at characterizing organisms as a continuous distribution of traits along biological gradients (Barton *et al.*, 2013; Violle *et al.*, 2014). However, when the goal is to gain mechanistic insight as to how organismal
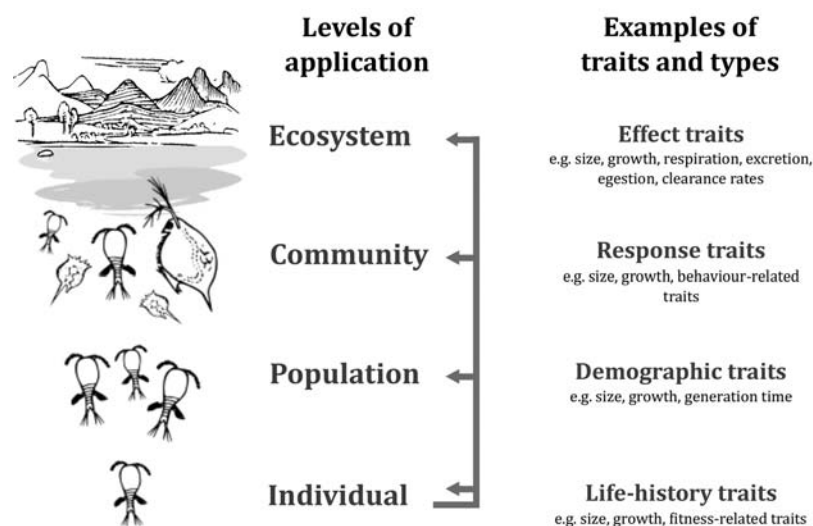

Fig. 1. Integrative framework linking functional trait classification across levels of biological organization (inspired from Violle et al., 2007). Particular trait types operate predominantly (but not exclusively) on processes at specific levels of biological organization, affecting individuals, populations, communities or ecosystems (i.e. level of application). Some traits affect several or all levels or organization and can thus be classified as multiple trait types (e.g. body size and growth).

presence and activity influence major biogeochemical cycles, the focus should instead shift toward effect traits, so as to incorporate feedbacks in ecosystems (e.g. Suding et al., 2008). In stark contrast to response traits, effect traits have been poorly described and applied in plankton ecology. Only very recently have two studies referred to plankton effect traits: Zwart et al. (2015), where taxon-specific values of phytoplankton light use efficiency were used in a trait-based model to predict lake primary productivity, and Litchman et al. (2015), where phytoplankton traits affecting biogeochemistry were reviewed. In their consideration of phytoplankton, this recent work provides strong cases revealing the relevance of effect traits in aquatic ecosystem ecology. However, the fact remains that effect traits are still rarely used, and the focus thus far, when it is on effect traits, has been for phytoplankton. We hereby call for an increased implementation of effect traits in plankton ecology, in particular for zooplankton, to remedy this situation.

Using effect traits to link zooplankton to ecosystem function

Adequately selecting effect traits implies a clear definition of the ecosystem function that is of interest. Although the term "ecosystem function" is used
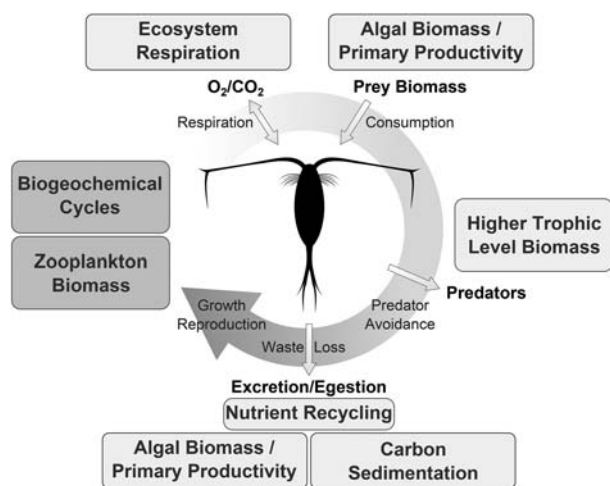

Fig. 2. Interactions of a typical herbivorous copepod with its environment, in terms of elemental and energy transfer. Inflows include prey and O_2 with outflows to predators, respired CO_2, and excreted or egested nutrients and organic matter. Organismal functions that regulate these exchanges are consumption, respiration, predator avoidance, waste/loss. Boxes indicate examples of ecosystem properties or processes that are influenced by these organismal functions. The circular arrow indicates that all organismal functions contribute to the overall individual goal of growth and reproduction, affecting zooplankton biomass directly, and biogeochemical cycles indirectly. Note that this concept can be transposed to other zooplankton taxa with other diet types.

pervasively in the literature, it is not always clearly defined; ecosystem function refers to the properties or processes of ecosystems. It is possible to decompose ecosystem functioning into: (i) the size of stocks of energy and material (e.g. biomass, batch nutrients), (ii) the flow of energy and transformation of material (e.g. primary or secondary productivity, decomposition of organic matter, nutrient recycling), and (iii) variation in the stocks and flows over time (Pacala and Kinzig, 2002). The potential influence of zooplankton on these ecosystem-level parameters has already been recognized, although largely outside of the functional ecology literature (Sirotnak and Huntly, 2000; Sterner, 2009). Zooplankton can impact the bioavailability of nutrients and energy flow in food webs through several direct and indirect pathways (Fig. 2). Direct effects represent changes occurring via the passage of elements through organisms, as a result of their bodily requirements: ingested elements are partially absorbed by the body for tissue growth and storage, with excesses released as metabolic waste via excretion or egestion (Vanni, 2002). Given their central trophic position in aquatic food webs, zooplankton also directly affect biomass stocks and community structure of their prey (via consumption) and predators (by being consumed), and thereby indirectly influence how other trophic levels affect ecosystem function (Fig. 2; Vanni, 2002). There are many examples of zooplankton modulation of elemental stocks and fluxes of carbon (C), nitrogen (N), and phosphorus (P) in the literature (e.g. Frangoulis et al., 2005; Steinberg and Saba, 2008; Alcaraz et al., 2010, 2014). While the existence of such data should allow for effect trait characterization across taxa, it should be noted that this information has mostly been made available for marine species (Hébert et al., 2016a); a bias that has likely constrained their use in freshwater studies.

Zooplankton effect traits should thus most likely include measurements related to organismal biomass and body composition (e.g. size and elemental requirements), and physiology (e.g. material fluxes over time such as growth, feeding, respiration, ingestion or excretion rates); traits that best capture the elemental exchanges between individuals and their environment (Calow, 1987; Allen and Polimene, 2011). For example, using stoichiometric metrics to describe zooplankton community structure can inform on nutrient transfer through food webs (e.g. based on relative body content of species groups; Andersen and Hessen, 1991; Sterner et al., 1992), while physiological characters of zooplankton can be used to predict ecosystem processes such as nutrient recycling, primary productivity or carbon export (Jawed, 1973; Urabe et al., 1995; Tamelander

Table I: Examples of hard effect traits and soft (proxy) traits in zooplankton and their potential impact on ecosystem processes (fluxes of energy and material)

Hard effect trait	Soft trait (proxy)	Ecosystem process
Growth rate	Body length Body mass Biovolume	Secondary productivity Carbon cycling
Feeding (clearance or grazing) rate	Body mass Feeding mode or apparatus	Nutrient and energy transfer (from prey to predator) Primary productivity
Sloppy feeding	Feeding mode	Nutrient recycling Heterotrophic bacterial productivity
Excretion rate	Body mass	Nutrient recycling Heterotrophic bacterial productivity Primary productivity
Faecal pellet production and sedimentation rates	Body length Body mass	Nutrient vertical export (translocation) Carbon sedimentation/cycling
Respiration rate	Body mass	Ecosystem respiration Carbon cycling

et al., 2012). However, these traits are infrequently used in trait-based studies, largely because data remain limited across many taxa (especially for freshwater species; Hébert *et al.*, 2016a), with measurements of body composition and physiological traits being more difficult and expensive to analyse: these are considered "hard" traits (Hodgson *et al.*, 1999). Although less mechanistically correlated with precise functions, more readily measured "soft" traits can sometimes be used as surrogate metrics to infer hard traits (Table I; Hodgson *et al.*, 1999; Nock *et al.*, 2016). Well-established trait-body size relationships could in this way alleviate the lack of effect trait data, e.g. for excretion, respiration (Ikeda *et al.*, 2001) or clearance rates (Barnett *et al.*, 2007; Table I). The limited use of effect trait metrics may also reflect a lack of communication between aquatic subfields, with community ecologists using trait-based approaches to characterize community structure with less concern for impacts on aggregate processes, and eco-physiologists and ecosystem ecologists focusing on organismal metabolism and stoichiometry with regard to biogeochemistry (the latter being more widespread in marine studies). As advocated by terrestrial ecologists (Lavorel and Garnier, 2002; Suding *et al.*, 2008), a clear distinction between response and effect trait applications would also help better integrate various subfields of aquatic ecology and stimulate collaborations.

Body size as a proxy for effect traits

Body size transcends multiple organismal functions, determining fitness and much of the ecology of zooplankton (Litchman *et al.*, 2013). Several corporeal properties and physiological rates scale with size, such as the total body content in energy and elements, feeding, excretion, and basal metabolism, all of which directly affect ecosystem stocks and/or fluxes (Fig. 2). To some extent, most biological rates increase as a function of body mass following a power law (Kleiber, 1961; Peters, 1983), after accounting for ambient temperature (Brown *et al.*, 2004). Thus, individual size is a major determinant of other traits, including several effect traits that also influence ecosystem function (Table I). Body size can be expressed in many possible units or energy currencies and be used as an indicator of informative hard traits. For example, length:mass ratios indicate body shape and mass:volume ratios indicate body density; features that can be related to zooplankton feeding and vertical transport (Litchman *et al.*, 2013). Further, body mass expressed in carbon, joules or calories can be used as a common energetic currency for bioenergetic modelling, e.g. to assess consumer–resource interactions or biomass ratios under changing conditions (Gilbert *et al.*, 2014). Importantly, size is also the typical denominator for most physiological rates (e.g. excretion, respiration) and, combined with mass-scaled exponents or empirical relationships for such rates (e.g. Ikeda *et al.*, 2001; Kiørboe and Hirst, 2014), body size can provide quantitative estimates of organismal contribution to elemental flow (e.g. N, P, and C; Frangoulis *et al.*, 2005; Alcaraz *et al.*, 2010). As a result, individual body size is both an important descriptor for zooplankton communities, providing information on overall biomass and size structure related to abiotic and biotic gradients, but equally, holding the potential for broader application for predicting ecosystem properties and processes (Yvon-Durocher and Allen, 2012).

Allometric mass–length equations and mass-scaled exponents of physiological rates can be jointly used in trait-based approaches to model the effects of particular communities on specific processes. For example, abundance and body length data can be converted to biomass using allometric equations and, combined with mass-specific metabolism data, it is possible to quantify overall community respiratory fluxes and thereby evaluate biotic contributions to ecosystem C-cycling (as shown in reef-fish communities by Barneche *et al.*, 2014, for example). Similar relationships could be established with plankton community matrices and trait databases (for trait compilations, see: Barnett *et al.*, 2007; Edwards *et al.*, 2015; Hébert *et al.*, 2016b), linking

plankton species to large-scale nutrient fluxes through community structure. However, care should be taken to not extrapolate trait relationships based on size beyond the size spectrum covered by particular established equations. Likewise, using mass-scaled exponents derived from extremely large size spectra, for example the general ¾ power law, to estimate any physiological rates can result in inaccurate predictions (Finkel *et al.*, 2004; Tilman *et al.*, 2004; Glazier, 2006; Alcaraz, 2016). To some extent, certain allometric exponents and size–trait relationships may be taxon- or habitat-specific (Rall *et al.*, 2011; Hébert *et al.*, 2016a). Other traits of equal relevance can be included to increase predictive power and accuracy (e.g. De Bie *et al.*, 2012). Despite these caveats, when no direct measurements of physiological traits are possible, body size information combined with adequate size–trait relationships can provide at least a rough estimate for important effect traits.

A BIOENERGETIC PERSPECTIVE ON ZOOPLANKTON EFFECT TRAITS

Energy allocation as a trait classification framework

Linking particular aspects of zooplankton to ecological processes likely requires a description of community composition in terms of functional traits. The scale of interest however determines the type of traits that are to be included in a classification. Litchman *et al.* (2013) proposed a categorization based on fundamental fitness components of organisms: feeding, growth, reproduction and survival. We propose expanding this classification by first decomposing these fundamental needs into energy allocation compartments, thereby more fully integrating physiological traits, and second, extending the scope of the functional trait framework to facilitate the identification of
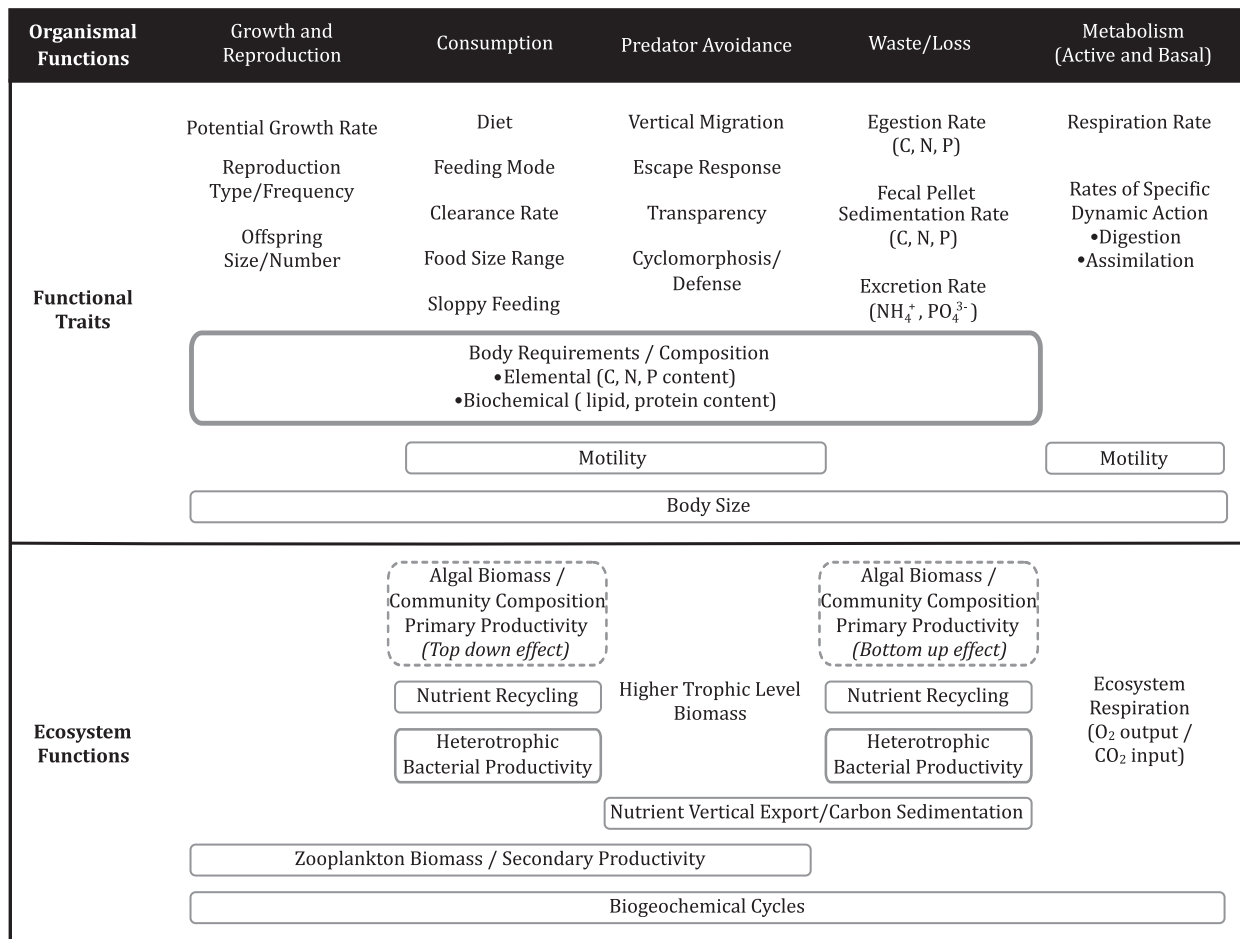

Fig. 3. A non-exhaustive classification of zooplankton functional traits (upper part) based on the energy budget of an individual (organismal functions), aligned with their respective impact at the ecosystem scale (ecosystem functions; lower part). Functional traits that transcend more than one organismal function are framed with solid lines; likewise, zooplankton trait-influenced ecosystem functions transcending organismal functions are also framed with solid lines. Frames with dotted lines indicate the bidirectional control (top-down and bottom-up) on the algal communities. This scheme expands on Litchman et al. (2013).

effect traits likely to affect ecosystem functioning. Our expanded framework (Fig. 3) categorizes traits based on the organismal functions they fulfil and represents the balance maintained between energy consumption and allocation to (active and basal) metabolism, growth and reproduction, with energy losses to excretion, egestion (Kiørboe *et al.*, 1985; Bâmstedt, 1988) and investment in anti-predator strategies (Visser, 2007; Kiørboe and Jiang, 2013). Our trait classification is thus based on a typical zooplankter's energy budget (with energy compartments hereafter referred to as organismal functions) in the top half of Fig. 3, and explicitly links traits to particular ecosystem functions likely to be affected, represented in the bottom half.

As highlighted by Litchman *et al.* (2013), some traits such as motility and body size transcend several organismal functions. Our framework demonstrates that effect traits related to body composition may also do so (Fig. 3). In this classification some functional traits, more commonly considered as response traits in plankton studies (i.e. traits governing how species abundances vary under environmental conditions), may equally be regarded as effect traits if they also have implications for ecosystem functioning (Fig. 3). Different effect traits can influence the same ecosystem process in different, and sometimes opposing ways (Figs 2 and 3). For example, through feeding, zooplankton exert top-down control on algal biomass, reducing phytoplankton standing stock and influencing their community composition; yet, zooplankton also sustain the growth and biomass of phytoplankton via nutrient excretion which enhances primary productivity (Figs 2 and 3; Lehman and Sandgren, 1985; Sterner, 2009). Other effect traits such as sloppy feeding and faecal pellet production may also simultaneously contribute to nutrient and C-cycling (Møller and Nielsen 2001; Wexels Riser *et al.*, 2008). Alternatively, a single trait may also influence several ecosystem functions: zooplankton excretion regenerates nutrient stocks, providing dissolved inorganic compounds for primary producers, but also supports heterotrophic bacterial growth (Fig. 3; Jumars *et al.*, 1989; Carlson, 2002). Changes in zooplankton community composition can also directly affect ecosystem stoichiometry through shifts among taxa of different elemental content (e.g. high P requirements in *Daphnia* as opposed to other taxa), which in turn affect relative release through excretion or egestion (Sterner and Elser, 2002). Ultimately, ecosystem storage and fluxes modulated by zooplankton biomass and activity all contribute to larger biogeochemical cycles, either directly or indirectly (Figs 2 and 3). The magnitude of this contribution is subject to variation however, obviously depending on overall plankton standing stocks and turnover, environmental conditions, ecosystem type and nutrient or carbon budget.

Assessing trait trade-offs through bioenergetics

Traits can acclimate and adapt in response to external forces, optimizing fitness by balancing energetic investment in different organismal functions (Calow and Townsend, 1981). Strong plankton trait trade-offs include energy investment in size versus growth (Sauterey *et al.*, 2015), in feeding versus hiding (Gliwicz, 2003), or in defense versus competition (Yoshida *et al.*, 2003). Energy allocation among organismal functions can be affected by environmental conditions (Calow and Sibly, 1983; Kiørboe, 2011), which alters favoured strategies and leads to differential upstream repercussions. Identifying and quantifying trait trade-offs can establish links within suites of organismal effect traits ("trait syndromes"; Poff *et al.*, 2006), with overall consequences for ecosystem function.

The energy-based trait classification we propose (Fig. 3) provides a reliable framework to further investigate energy compensation amongst multiple traits with potential implications for ecosystem processes; not only for zooplankton, but for multiple groups of heterotrophic organisms. For example, because higher temperatures increase metabolic rates related to zooplankton organismal functions across species (e.g. Ikeda *et al.*, 2001), greater basal metabolism can induce higher energy consumption and/or lower investment in growth or reproduction to maintain an overall energy balance (e.g. Kiørboe *et al.*, 1985). A potential outcome for ecosystems undergoing warming is a strengthening of consumer–resource interactions (O'Connor *et al.*, 2009), with zooplankton exerting stronger top-down control on primary producers (West and Post, 2016). However, if zooplankton individuals compensate for higher metabolic costs by consuming more, they will also excrete and thus recycle more nutrients, which could then benefit less edible phytoplankton species/primary producers (Miller and Landry, 1984). Such energetic trade-offs allow for clear *a priori* hypotheses to be framed and tested to further investigate the repercussions of linked effect traits on food web regulating processes (i.e. top-down versus bottom-up control) and ecosystem balance (e.g. stoichiometric pool/nutrient availability, productivity to respiration ratio). Hierarchical frameworks that clearly organize organismal energy allocation and associated effect traits along with ecological processes prone to be affected, such as the one provided in Fig. 3, are likely to be broadly applicable in this context.

CONCLUDING REMARKS

There are still many gaps in the zooplankton effect trait values available in the literature. Thus the most obvious

recommendation for future work is for more measurements and for making such data widely available, especially for less-studied taxa or habitats. More specifically, trait information is especially limited for freshwater species (Hébert *et al.*, 2016a) as well as in some less-studied areas such as the more diverse tropics (Castilho-Noll *et al.*, 2010). A recent compilation of reviewed taxa-specific values of zooplankton traits likely to influence C, N, and P stocks and fluxes in both marine and freshwater environments has been released, which can provide a base to be expanded upon (Hébert *et al.*, 2016b). Increasing data availability on effect traits will not only help incorporate more mechanistic metrics in plankton community–ecosystem functioning linkages, but may also improve our ability to quantify and parameterize intra- and inter-specific trait variation and trade-offs, under static versus changing environmental conditions in ecosystem modelling.

Ecosystem functioning is the emergent property of multiple environmental drivers and filters operating at a hierarchy of scales, with assemblages of individuals optimally acclimated to their habitat conditions (Lavorel and Garnier, 2002). Because functional traits may interact or synergistically influence different aspects of ecosystem functioning, identifying which traits are most relevant still remains a major challenge in functional ecology (Hooper *et al.*, 2005). In light of this challenge, we appeal to plankton ecologists to more clearly define their goals when developing trait-based approaches so as to facilitate the choice of traits in future studies. When the aim is to assess ecosystem-level properties or processes, functional effect traits with explicit, direct links between organisms and ecosystem function should be used; if the goal is to broadly determine how community composition may vary under changing conditions using traits instead of taxonomy, then response traits of interest should be identified. As trait-based ecology matures, we encourage the use of both response and effect traits, given that their joint implementation is relevant to assessing organismal feedbacks on ecosystems undergoing environmental change. Finally, we believe that using a bioenergetic approach as an alternative for trait categorization holds the potential to better link organismal activity to ecosystem function, offering an integrative framework to assess trait variation and trade-offs and their ecological repercussions.

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REFERENCES

Alcaraz, M. (2016) Marine zooplankton and the metabolic theory of ecology: is it a predictive tool? *J. Plankton Res.*, DOI:10.1093/plankt/fbw012.

Alcaraz, M., Almeda, R., Calbet, A., Saiz, E., Duarte, C. M., Lasternas, S., Agustí, S., Santiago, R., Movilla, J., Alonso, A. (2010) The role of arctic zooplankton in biogeochemical cycles: respiration and excretion of ammonia and phosphate during summer. *Polar Biol.*, **33**, 1719–1731.

Alcaraz, M., Almeda, R., Duarte, C. M., Horstkotte, B., Lasternas, S., Agustí, S. (2014) Changes in the C, N, and P cycles by the predicted salps-krill shift in the southern ocean. *Front. Mar. Sci.*, **1**, 1–13.

Allen, J. I. and Polimene, L. (2011) Linking physiology to ecology: towards a new generation of plankton models. *J. Plankton Res.*, **33**, 989–997.

Andersen, T. and Hessen, D. O. (1991) Carbon, nitrogen, and phosphorus content of freshwater zooplankton. *Limnol. Oceanogr.*, **36**, 807–814.

Arnold, S. J. (1983) Morphology, performance and fitness. *Am. Zool.*, **23**, 347–361.

Bâmstedt, U. (1988) Ecological significant of individual variability in copepod bioenergetics. *Hydrobiologia*, **167**, 43–59.

Barneche, D., Kulbicki, M., Floeter, S., Friedlander, A., Maina, J. and Allen, A. P. (2014) Scaling metabolism from individuals to fish communities at broad spatial scales. *Ecol. Lett.*, **17**, 1067–1076.

Barnett, A. J. and Beisner, B. E. (2007) Zooplankton biodiversity and primary productivity: explanations invoking resource abundance and distribution. *Ecology*, **88**, 1675–1686.

Barnett, A. J., Finlay, K. and Beisner, B. E. (2007) Functional diversity of crustacean zooplankton communities: towards a trait-based classification. *Freshwater Biol.*, **52**, 769–813.

Barton, A. D., Pershing, A., Litchman, E., Record, N. R., Edwards, K. F., Finkel, Z. V., Kiørboe, T. and Ward, B. (2013) The biogeography of marine plankton traits. *Ecol. Lett.*, **16**, 522–534.

Beisner, B. E. and Longhi, M. L. (2013) Niche overlap and diversity patterns in lake phytoplankton. *Limnol. Oceanogr.*, **58**, 1419–1430.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. and West, G. B. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771–1789.

Calow, P. (1987) Towards a definition of functional ecology. *Funct. Ecol.*, **1**, 57–61.

Calow, P. and Sibly, R. (1983) Physiological trade-offs and the evolution of life cycles. *Sci. Prog.*, **68**, 177–188.

Calow, P. and Townsend, C. R. (1981) Energetics, ecology and evolution. In: Townsend, C. R. and Calow, P. *Physiological Ecology*. Blackwell Scientific Publications, Oxford, pp. 3–19.

Carlson, C. A. (2002) Production and removal processes. In: Hansell, D. A. and Carlson, C. A. *Biogeochemistry of Marine Dissolved Organic Matter*. Academic Press, New York, pp. 91–151.

Castilho-Noll, M. S. M., Câmara, C. F., Chicone, M. F. and Shibata, E. H. (2010) Pelagic and littoral cladocerans (Crustacea, Anomopoda and Ctenopoda) from reservoirs of the northwest of São Paulo State, Brazil. *Biota Neotropica*, **10**, 1–10.

Chapin, F. S. III, Reynolds, H. L., D'Antonio, C. M. and Eckhart, V. M. (1996) The functional role of species in terrestrial ecosystems. In: Walker, B and Steffen, W. *Global Change and Terrestrial Ecosystems*. Cambridge University Press, Cambridge, UK, 403–428.

de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J. H. C., Bardgett, R. D., Berg, M. P. *et al.* (2010) Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodivers. Conserv.*, **19**, 2873–2893.

De Bie, T., De Meester, L., Brendonck, L., Martens, K., Goddeeris, B., Ercken, D., Hampel, H., Denys, L. *et al.* (2012) Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. *Ecol. Lett.*, **15**, 740–747.

Díaz, S. and Cabido, M. (2001) Vive la difference: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.*, **16**, 646–655.

Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., Robson, M. T. (2007) Incorporating plant functional diversity effects in ecosystem service assessements. *Proc. Natl. Acad. Sci. USA*, **104**, 20684–20689.

Edwards, K. F., Litchman, E. and Klausmeier, C. A. (2013a) Functional traits explain phytoplantkon community structure and seasonal dynamics in a marine ecosystem. *Ecol. Lett.*, **16**, 56–63.

Edwards, K. F., Litchman, E. and Klasumeier, C. A. (2013b) Functional traits explain phytoplankton responses to environmental gradients across lakes of the United States. *Ecology*, **94**, 1626–1635.

Edwards, K. F., Klasumeier, C. A. and Litchman, E. (2015) Nutrient utilization traits of phytoplankton. *Ecology*, **96**, 2311.

Eviner, V. T. and Chapin, F. S. III (2003) Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. *Annu. Rev. Ecol. Syst.*, **34**, 455–485.

Finkel, Z., Irwin, J. A. and Schofield, O. (2004) Resource limitation alters the ¾ scaling law of metabolic rates in phytoplankton. *Mar. Ecol. Prog. Ser.*, **273**, 269–270.

Frangoulis, C., Christou, E. D. and Hecq, J. H. (2005) Comparison of marine copepod outfluxes: nature, rate, fate and role in the carbon and nitrogen cycles. *Adv. Mar Biol.*, **47**, 254–309.

Gayraud, S., Statzner, B., Bady, P., Haybachp, A., Schöll, F., Usseglio-Polatera, P., Bacchi, M. (2003) Invertebrate traits for the biomonitoring of large European rivers: an initial assessment of alternative metrics. *Freshwater Biol.*, **48**, 2045–2064.

Gilbert, B., Tunney, T. D., McCann, K. S. , DeLong, J. P., Vasseur, D. A., Savage, V., Shurin, J. B., Dell, A. I. *et al.* (2014) A bioenergetic framework for the temperature dependence of trophic interactions. *Ecol. Lett.*, **17**, 902–914.

Giller, P. S., Hillebrand, H., Berninger, U. G., Gessner, M. O., Hawkins, S., Inchausti, P., Inglis, C., Leslie, H. *et al.* (2004) Biodiversity effects on ecosystem functioning: emerging issues and their experimental test in aquatic environments. *Oikos*, **104**, 423–436.

Glazier, D. S. (2006) The 3/4-power law is not universal: evolution of isometric, ontogenetic metabolic scaling in pelagic animals. *BioScience*, **56**, 325–332.

Gliwicz, Z. M. (2003) *Between Hazards of Starvation and Risk of Predation: The Ecology of Offshore Animals*. International Ecology Institute, Nordbünte, Germany.

Hébert, M-P., Beisner, B. E. and Maranger, R. (2016a) A meta-analysis of zooplankton functional traits influencing ecosystem function. *Ecology*, **97**, 1069–1080.

Hébert, M-P., Beisner, B. E. and Maranger, R. (2016b) A compilation of quantitative functional traits for marine and freshwater crustacean zooplankton. *Ecology*, **97**, 1081.

Hodgson, J. G., Wilson, P. J., Hunt., R. *et al.* (1999) Allocating C-S-R plant functional types: a soft approach to a hard problem. *Oikos*, **85**, 282–294.

Hooper, D. U., Chapin, F. S. III, Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M. *et al.* (2005) Effects of biodiversity on ecosystem functioning a consensus of current knowledge. *Ecol. Monogr.*, **75**, 3–35.

Ikeda, T., Kanno, Y., Ozaki, K. and Shinada, A. (2001) Metabolic rates of epipelagic marine copepods as a function of body mass and temperature. *Mar. Biol.*, **139**, 587–596.

Jawed, M. (1973) Ammonia excretion by zooplankton and its significance to primary productivity during summer. *Mar. Biol.*, **23**, 115–120.

Jumars, P. A., Penry, D. L., Baross, J. A., Perry, M. J. and Frost, B. W. (1989) Closing the microbial loop: dissolved carbon pathway to heterotrophic bacteria from incomplete ingestion, digestion and absorption in animals. *Deep-Sea Res. I*, **36**, 483–495.

Kearney, M. and Porter, W. (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.*, **12**, 1–17.

Kiørboe, T. (2011) How zooplankton feed: mechanisms, traits and tradeoffs. *Biol. Rev.*, **86**, 311–340.

Kiørboe, T. and Hirst, A. G. (2014) Shifts in mass scaling of respiration, feeding, and growth rates across life-form transitions in marine pelagic organisms. *Am. Nat.*, **183**, E118–E130.

Kiørboe, T. and Jiang, H. (2013) To eat and not be eaten: optimal foraging behavior in suspension feeding copepods. *J. R. Soc. Interface*, **10**, 20120693, doi:10.1098/rsif.2012.0693.

Kiørboe, T, Mohlenberg, F. and Hamburger, K. (1985) Bioenergetics of the planktonic copepod Acartia tonsa: relation between feed ing, egg production and respiration, and composition of specific dynamic action. *Mar. Ecol. Prog. Ser.*, **26**, 85–97.

Kleiber, M. (1961) *The Fire of Life: An Introduction to Animal Energetics*. Wiley, New York.

Lavorel, S. and Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.*, **16**, 545–556.

Lehman, J. T. and Sandgren, C. D. (1985) Species-specific rates of growth and grazing loss among freshwater algae. *Limnol. Oceanogr.*, **30**, 34–46.

Le Quéré, C., Harrison, S. P., Prentice, I. C., Buitenhuis, E. T., Aumont, O., Bopp, L., Claustre, H., Cotrim Da Cunha, L. (2005) Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models. *Glob. Change Biol.*, **11**, 2016–2040.

Litchman, E., de Tezanos Pinto, P., Klausmeier, C. A. *et al.* (2010) Linking traits to species diversity and community structure in phytoplankton. *Hydrobiologia*, **653**, 15–38.

Litchman, E., de Teznos Pinto, P., Edwards, K. F., Klausmeier, C. A., Kremer, C. T. and Thomas, M. K. (2015) Global biogeochmical impacts of phytoplankton: a trait-based perspective. *J. Ecol.*, **103**, 1384–1396.

Litchman, E. and Klausmeier, C. A. (2008) Trait-based community ecology of phytoplankton. *Ann. Rev. Ecol. Evol. Syst.*, **39**, 615–639.

Litchman, E., Klausmeier, C.A., Schofield, O. M. and Falkowski, P. G. (2007) The role of functional traits and trade-offs in structuring phytoplankton communities: scaling from cellular to ecosystem level. *Ecol. Lett.*, **10**, 1170–1181.

Litchman, E., Ohman, M. D. and Kiørboe, T. (2013) Trait-based approaches to zooplankton communities. *J. Plankton Res.*, **35**, 473–484.

Mcgill, B. J., Enquist, B. J., Weiher, E. and Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends Ecol. Evol.*, **21**, 178–185.

Merico, A., Bruggeman, J. and Wirtz, K. (2009) A trait-based approach for downscaling complexity in plankton ecosystem models. *Ecol. Model.*, **220**, 3001–3010.

Miller, C. A. and Landry, M. R. (1984) Ingestion-independent rates of ammonium excretion by the copepod Calanus pacificus. *Mar. Biol.*, **78**, 265–270.

Møller, E. F. and Nielsen, T. G. (2001) DOM production by marine copepods: effect of phytoplankton biomass and cell size. *J. Plankton Res.*, **23**, 527–536.

Nock, C. A., Vogt, R. J. and Beisner, B. E. (2016) Functional traits. *eLS*. John Wiley & Sons, Ltd., Chichester, DOI:10.1002/9780470015902.a0026282.

O'Connor, M. I., Piehler, M. F., Leech, D. M., Anton, A. and Bruno, J. F. (2009) Warming and resource availability shift food web structure and metabolism. *PLoS Biol.*, **7**, e1000178.

Pacala, S. and Kinzig, A. P. (2002) Introduction to theory and the common ecosystem model. In: Pacala, S, Kinzig, A. P. and Tilman, D *The Functional Consequences of Biodiversity: Empirical Process and Theoretical Extensions.* Princeton University Press, New York, pp. 169–174.

Petchey, O. L. and Gaston, K. J. (2002) Functional diversity (FD), species richness, and community composition. *Ecol. Lett.*, **5**, 402–411.

Petchey, O. L. and Gaston, K. J. (2006) Functional diversity: back to basics and looking Forward. *Ecol. Letters*, **9**, 741–758.

Peters, R. H. (1983) *The Ecological Consequences of Body Size.* Cambridge University Press, New York.

Poff, N. L., Olden, J. D., Vieira, N. K. M., Finn, D. S., Simmons, M. P., Kondratieff, B. C. (2006) Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. *J. N. Am. Benthol. Soc.*, **25**, 730–755.

Rall, B. C., Kalinkat, G., Ott, D., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M. (2011) Taxonomic versus allometric constraints on non-linear interaction strengths. *Oikos*, **120**, 483–492.

Reynolds, C. S., Huszar, V., Kruk, C., Naselli-Flores, L., Melo, S. (2002) Towards a functional classification of the freshwater phytoplankton. *J. Plankton Res.*, **24**, 417–428.

Sæther, B.-E. and Bakke, Ø. (2000) Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology*, **81**, 642–653.

Sauterey, B., Ward, B. A., Follows, M. J., Bowler, C. and Claessen, D. (2015) When everything is not everywhere but species evolve: an alternative method to model adaptive properties of marine ecosystems. *J. Plankton Res.*, **37**, 28–47.

Sirotnak, J. M. and Huntly, N. J. (2000) Direct and indirect effects of herbivores on nitrogen dynamics: voles in riparian areas. *Ecology*, **81**, 78–87.

Steinberg, D. K. and Saba, G. K. (2008) Nitrogen consumption and metabolism in marine zooplankton. *Nitrogen in the Marine Environment.* 2nd Edition. Academic Press/Elsevier, San Diego, CA, USA1135–1196.

Sterner, R. W. (2009) Role of zooplankton in aquatic ecosystems. In Likens, G. E. (ed.), *Encyclopedia of inland waters.* 1st edition. Elsevier, Oxford, UK, 678–688.

Sterner, R. W. and Elser, J. J. (2002) *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere.* Princeton University Press, Princeton.

Sterner, R. W., Elser, J. J. and Hessen, D. O. (1992) Stoichiometric relationships among producers, consumers, and nutrient cycling in pelagic ecosystems. *Biogeochemistry*, **17**, 49–67.

Suding, K. N., Lavorel, S., Chapin, F. S. III, Cornelissen, J. H. C., Díaz, S., Garnier, E., Goldberg, D., Hooper, D. *et al.* (2008) Scaling environmental change through the community-level: a trait-based response-and effect framework for plants. *Glob. Change Biol.*, **14**, 1125–1140.

Tamelander, T., Aubert, A. B. and Wexels Riser., C. (2012) Export stoichiometry and contribution of copepod fecal pellets to vertical flux of particulate organic carbon, nitrogen and phosphorus. *Mar. Ecol. Prog. Series*, **459**, 17–28.

Thomas, M. K., Kremer, C. T. and Litchman, E. (2016) Environment and evolutionary history determine the global biogeography of phytoplankton temperature traits. *Global Ecol. Biogeogr.*, **25**, 75–86.

Tilman, D., Hillerislambers, J., Harpole, S. , Dybzinski, R., Fargione, J., Clark, C., Lehman, C. (2004) Does metabolic theory apply to community ecology? It's a matter of scale. *Ecology*, **85**, 1797–1799.

Urabe, J., Nakashini, M. and Kawabata., K. (1995) Contribution of metazoan plankton to the cycling of nitrogen and phosphorus in Lake Biwa. *Limnol. Oceanogr.*, **40**, 232–241.

Vanni, M. (2002) Nutrient cycling by animals in freshwater ecosystems. *Annu. Rev. Ecol. Syst.*, **33**, 341–370.

Violle, C., Navas, M., Vile, D., Kazakou, E., Fortunel, C., Hummel, I, Garnier, E. (2007) Let the concept of trait be functional! *Oikos*, **116**, 882–892.

Violle, C., Reich, P. B., Pacala, S. W., Enquist, B. J., Kattge, J. (2014) The emergence and promise of functional biogeography. *Proc. Natl. Acad. Sci. USA*, **111**, 13690–13696.

Visser, A. W. (2007) Motility of zooplankton: fitness, foraging and predation. *J. Plankton Res.*, **29**, 447–461.

West, D. C. and Post, D. M. (2016) Impacts of warming revealed by linking resource growth rates with consumer functional response. *J Animal Ecol.*, **85**, 671–680.

Wexels Riser, C., Wassmann, P., Reigstad, M. and Seuthe, L. (2008) Vertical flux regulation by zooplankton in the northern Barents Sea during arctic spring. *Deep-Sea Res. I*, **55**, 2320–2329.

Yoshida, T., Jones, L. E., Ellner, S. P., Fussmann, G. F. and Hairston, N. G. Jr. (2003) Rapid evolution drives ecological dynamics in a predator-prey system. *Nature*, **424**, 303–306.

Yvon-Durocher, G. and Allen, A. P. (2012) Linking community size structure and ecosystem functioning using metabolic theory. *Philos. Trans. R. Soc. B*, **367**, 2998–3007.

Zwart, J. A., Solomon, C. T. and Jones, S. E. (2015) Phytoplankton traits predict ecosystem function in a global set of lakes. *Ecology*, **96**, 2257–2264.